Biology of *Andrena* (*Callandrena* sensu lato) *asteris* Robertson (Hymenoptera: Andrenidae), an Eastern Aster Specialist that Makes a Very Deep Nest

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Abstract - Here we present the first description of nest architecture, immature stages, and brood-parasitism of *Andrena* (*Callandrena* s. l.) *asteris* (Aster Miner Bee) and the first description of the nesting biology of any *Callandrena* in eastern North America. Brood cells varied from 50 to 91 cm in depth, making this the deepest solitary bee nest recorded in northeastern North America. Additionally, we assembled data on soil texture, phenology, geographic distribution, and host-plant preferences. By modeling publicly available observation data, we find that areas of peak habitat suitability for *A. asteris* are in proximity to coastal and inland shorelines and major water courses. Our results corroborate a recent assessment of the conservation status of New York pollinators, which ranked *A. asteris* as "vulnerable".

Introduction

Andrena is one of the largest genera of bees, with ~1500 valid species and an estimated 500 more yet to be described (Dubitzky et al. 2010). All members of this genus are solitary or communal, and ground-nesting. They range from narrow host-plant specialists that only consume pollen from a few species (e.g., *Andrena astragali* Viereck and Cockerell [Death Camas Miner Bee]; Cane 2018) to more broadly polylectic species, which visit a variety of host-plant families (Wood and Roberts 2017, 2018). *Andrena* is most diverse in arid regions such as the North American Southwest, the Mediterranean basin, and the steppes of Central Asia (Dubitzky et al. 2010). The genus *Andrena* diverged an estimated 20 million years ago and, along with their brood parasites in the genus *Nomada* (Apidae), is one of the most rapidly diversifying lineages of bees (Bossert et al. 2021).

In eastern North America, *Andrena* species fall into 3 broad ecological groups: spring-flying species foraging predominantly on trees that flower in early spring, spring-flying species specializing on herbaceous ephemerals, and summer-flying species specializing on herbaceous prairie plant species (Wood and Roberts 2018). In a study of Michigan *Andrena*, Wood and Roberts (2018) found that roughly half (48%) were host-plant specialists, primarily on plants in the families Asteraceae, Geraniaceae, Hydrophyllaceae, and Montiaceae. Host-plant specialization is more common in North America than in the Palearctic region, such as Britain, where only around 36% of the species are oligolectic (Wood and Roberts 2017).

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Callandrena is the largest exclusively North American subgenus of *Andrena* with 86 described species (see Table S1 in Supplemental File 1, available online at https://www.eaglehill.us/NENAonline/suppl-files/n29-4-N1991-Espinoza-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/N1991.s1), 14 of which occur east of the Mississippi, and 12 of which occur in New York (see Table S1 in Supplemental File 1; Ascher and Pickering 2021). *Callandrena* is most diverse in the southwestern United States and Mexican plateau (see Table S1 in Supplemental File 1; LaBerge 1967). All *Callandrena* collect pollen exclusively from Asteraceae (LaBerge 1967).

The subgenus *Callandrena*, as originally defined, is now known to be a paraphyletic group, based on multiple phylogenetic analyses (Bossert et al. 2021, Larkin et al. 2006, Pisanty et al. 2021). *Callandrena* in the narrow sense (i.e., *Callandrena* sensu stricto), including the type species, *Andrena manifesta* (Fox), was recovered as part of a monophyletic group referred to as Group A by Larkin et al. (2006) and Clade 4 by Pisanty et al. (2021). Many other species, previously referred to as *Callandrena*, belong to another, unrelated (and currently unnamed) group (referred to as Group B,C,D by Larkin et al. [2006] and Clade 12 by Pisanty et al. [2021]). *Andrena asteris* Robertson (Aster Miner Bee) belongs to this second, unnamed group. The morphological characters traditionally used to group these 2 distantly related groups of "*Callandrena*", such as highly branched scopal hairs, presumably arose as a consequence of their shared use of Asteraceae pollen (Larkin et al. 2006).

Most previous studies of "*Callandrena*" nesting biology have been conducted on species that are in the unnamed group. Given the uncertainty surrounding *Andrena* subgeneric classification, we refer to *A. asteris* as belonging to "*Callandrena* sensu lato" until a proper taxonomic name is applied to the subgroup recognized as Larkin's Group B,C,D and Pisanty's Clade 12. See Table S1 in Supplemental File 1 for group affiliations for all of the 86 currently described species in *Callandrena* sensu lato.

All previous studies of nesting biology and life history of members of *Callandrena* s.l. were conducted in the western United States (Neff and Simpson 1997, Parker and Bohart 1982, Parker and Griswold 1982, Rozen 1973). To the best of our knowledge, this is the first paper to document nesting biology of a species of *Callandrena* s.l. in eastern North America.

Andrena asteris (Fig. 1a) is a late summer/early fall bee, active in September and October in the northeastern United States. It has been recorded collecting pollen on various species of *Symphyotrichum* and *Solidago* (LaBerge 1967). Very little else is known about this species, as its nesting behavior has never been studied. Here we present new information on the nest architecture, immature stages, pollen usage, and likely brood-parasitism of *A. asteris*.

Field Site Description

We conducted our field study from 22 September to 3 October 2020. The site is located on a glacial moraine ~4.8 km (3 mi) southwest of Cortland, Tompkins County, NY (42°33'22"N, 76°13'42"W; Fig. 2). The center of our study site consists of an open meadow surrounded by poplar trees. Flowers blooming at the time of

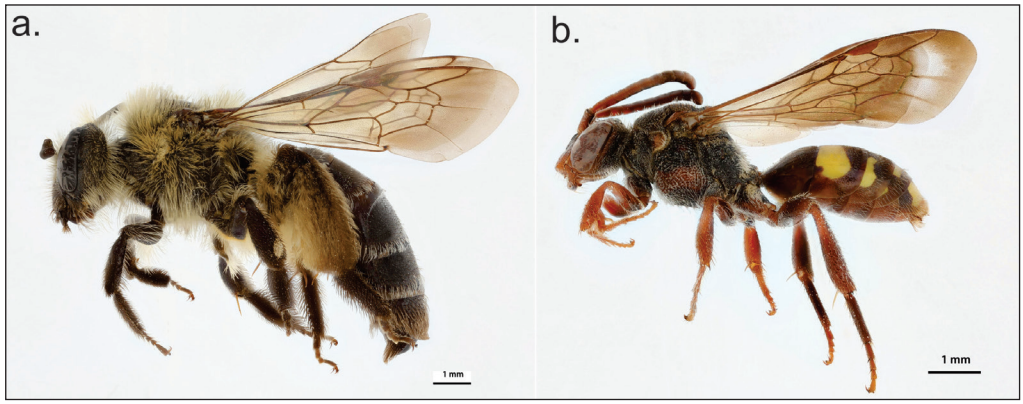

Figure 1. (a) Female *Andrena asteris*, lateral view, and (b) female *Nomada banksi*, lateral view.

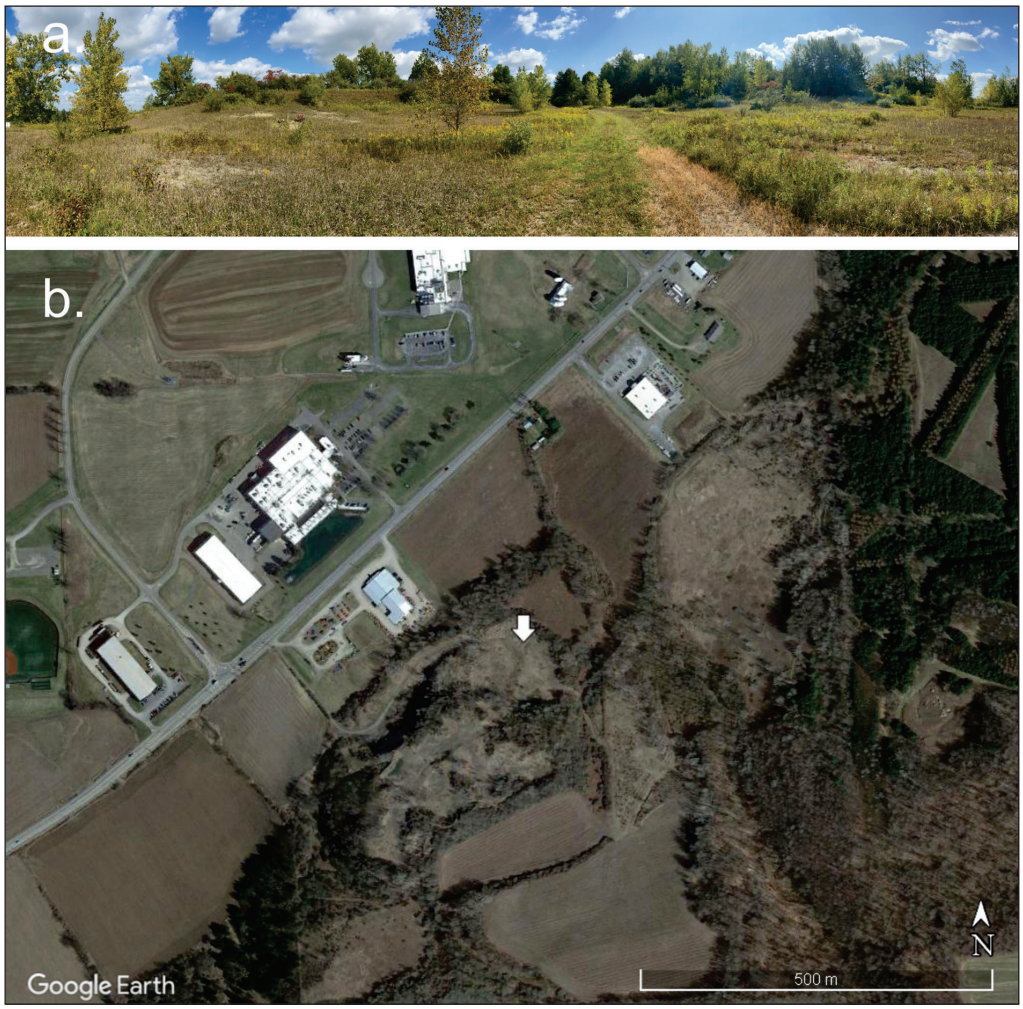

Figure 2. (a) panoramic view of field site, and (b) Google Earth image of field site; arrow indicates location of nests.

A. asteris activity included *Daucus carota* L. (Wild Carrot), *Euthamia graminifolia* (L.) Nuttall (Grass-leaved Goldenrod), *Symphyotrichum novae-angliae* (L.) Nesom (New England Aster), *Symphyotrichum lateriflorum* (L.) Löve and Löve (Calico Aster), *Lotus corniculatus* L. (Bird's-foot Trefoil), and multiple *Solidago* species (hereafter, *Solidago* spp.). Nests of *A. asteris* were located in exposed patches of sand. The area in which nests were located was southwest-facing and gently sloping; we did not find any nests in the adjacent flatter and wetter portion of the meadow. The soil at this site is classified as Valois and Howard gravelly loams (NRCS 2019). Other Apoidea found nesting at the site included bees in the genus *Lasioglossum*, *Halictus ligatus* Say (Halictidae), *Melissodes druriellus* (Kirby) (Drury's Long-horned Bee; Apidae), and abundant solitary, hunting wasps, including *Cerceris fumipennis* Say (Crabronidae), a predator of buprestid beetles (Swink et al. 2013). There were also a few dozen *Apis mellifera* L. (Honey Bee) hives at the northern edge of the clearing.

Methods

Phenology and geographic distribution

We used publicly available data from the Global Biodiversity Information Facility (GBIF), Symbiota Collections of Arthropods Network (SCAN), and the American Museum of Natural History's Arthropod Easy Capture Specimen database (AMNH-AEC) to characterize the phenological activity and the known geographic distribution of *A. asteris*. We downloaded data in June 2021, then inspected the data and removed duplicate and suspect specimen records. In the end, we obtained 456 observations that included reliable phenological and geographic data (see Table S2 in Supplemental File 1). We used these records to plot both the period of adult activity as well as the known geographic range using R (version 4.1.2) and QGIS(version 3.16) (QGIS.org 2022, R Core Team 2021).

In order to further characterize the geographic range and habitat suitability of *A. asteris*, we used the package 'MaxEnt' (v3.4.3; Phillips et al. 2022), through the package 'ENMeval' (v2.0; Kass et al. 2021). In R, we combined occurrence data from the 3 repositories described above and filtered to retain occurrence records between 1981 and 2010 to align with the climatology data obtained through CHELSA (v2.1; Karger et al. 2017), leaving 31 occurrence records. We first checked records against a gazetteer to identify and exclude occurrence records with georeferencing errors using the package 'CoordinateCleaner' (version 2.0-20; Zizka et al. 2019). We thinned the remaining occurrence records to 10 km with the package 'spThin' (version 0.2.0) to reduce the effects of spatial sampling bias (Aiello-Lammens et al. 2015, Radosavljevic and Anderson 2014, Sillero and Barbosa 2021). To account for the role of the climate and nest-site availability on the distribution of *A. asteris*, we included bioclimatic variables derived from the 1981–2010 climate normals (Karger et al. 2017) and soil-texture data (Hengl 2018a, 2018b) as environmental covariates (see Table S3 in Supplemental File 1). We performed principal components analysis on these covariates to (i) limit the potential impacts of collinearity, even though 'MaxEnt' is thought to be robust to collinearity when not extrapolating

across space or time (de Marco and Nobrega 2018, Feng et al. 2019), and (ii) to reduce dimensionality by including components up to a threshold of 95% of variance explained. Finally, we trained the models using both block and jackknife partitioning of the presence data and assigned random background points to 30% of the background pixels (~24,600 points). We evaluated model performance with area under the curve (AUC) and Akaike information criterion corrected for small sample size (AICc), which we compared to 100 iterations of the null model generated through 'ENMeval'.

Nest architecture and soil-texture analysis

We located nest entrances by observing female bees who were actively provisioning brood cells and thus could be seen making regular trips to and from nests. We placed a clear plastic cup over the nest entrance after female bees entered their nests, and then collected the bees as they emerged several minutes later. We identified these specimens with the Discover Life *Andrena* female key (Ascher and Pickering 2020) and compared them to other *A. asteris* in the Cornell University Insect Collection (CUIC) for confirmation. Voucher specimens were deposited in the CUIC.

We excavated a total of 5 nests, starting at the entrance and exposing the side of the tunnel down to the brood cells using the methods described in Rozen et al. (2019). We blew talcum powder into the tunnel to line the tunnel walls and used a pocket knife and trowel to scrape away the soil. We measured the tunnel diameter, length and width of brood cells, lateral length (distance of a brood cell from the main tunnel), and diameter of tunnels for pollen provision using a tape measure, digital calipers, and a pipefitter's small-hole gauge. Dimensions of nests and brood cells are herein expressed as mean ± standard deviation. We submitted soil samples collected from the surface and the brood-cell depth of each for particle-size analysis to the Cornell Soil Health Laboratory (https://soilhealth.cals.cornell.edu/).

Pollen analysis

To aid in pollen identification, we collected reference pollen from all flowers observed blooming within 100 m of the nest site in September 2021. We analyzed pollen provisions from 3 different brood cells. We first homogenized each provision mass by vortexing in 70% ethanol, and then randomly took 3 subsamples from each provision. For each subsample, we pipetted 70 µL of the pollen suspension onto a microscope slide, added several drops of Calberla's solution to dye the grains, and added a coverslip. We examined pollen grains at 200x magnification on a compound Olympus BX41 microscope (Olympus Corp. Tokyo, Japan) with CellSens® software (Olympus Corp.). We randomly initiated 10 unique transects along the short edge of the coverslip and examined all pollen grains that were fully visible in the field of view for the full length of the coverslip. We compared pollen morphospecies from the brood provisions to the reference photos and took multiple voucher photos. Due to the exceptional difficulty of differentiating Asteraceae pollen, and the lack of keys for the *Solidago* and *Symphyotrichum* groups (e.g., Faegri et al. 1989, Punt and Hoen 2009), we measured multiple traits on

pollen reference photos of New England Aster, Calico Aster, *Solidago* spp., and Grass-leaved Goldenrod in an attempt to identify distinguishing characters. Traits included length of polar and orbital axes, polar-to-orbital axis ratio, spine length, furrow depth, and number of spines visible from polar view (see Figs. S1, S2 in Supplemental File 2,available online at https://www.eaglehill.us/NENAonline/suppl-files/n29-4-N1991-Espinoza-s2, and for BioOne subscribers, at https://www.doi.org/10.1656/N1991.s2).

Results

Phenology and geographic distribution

Museum records extending from 1890 to the present indicate that *A. asteris* is a late-summer bee that has been primarily collected from August through October, with peak collections occurring in September (Fig. 3). Based on historical records, the range of *A. asteris* stretches from Ontario southward to Mississippi and from Nova Scotia westward to North Dakota (Fig. 4).

For species-distribution modeling, we tested 25 combinations of model parameters with 2 partitioning methods for the predicted habitat model. The highest

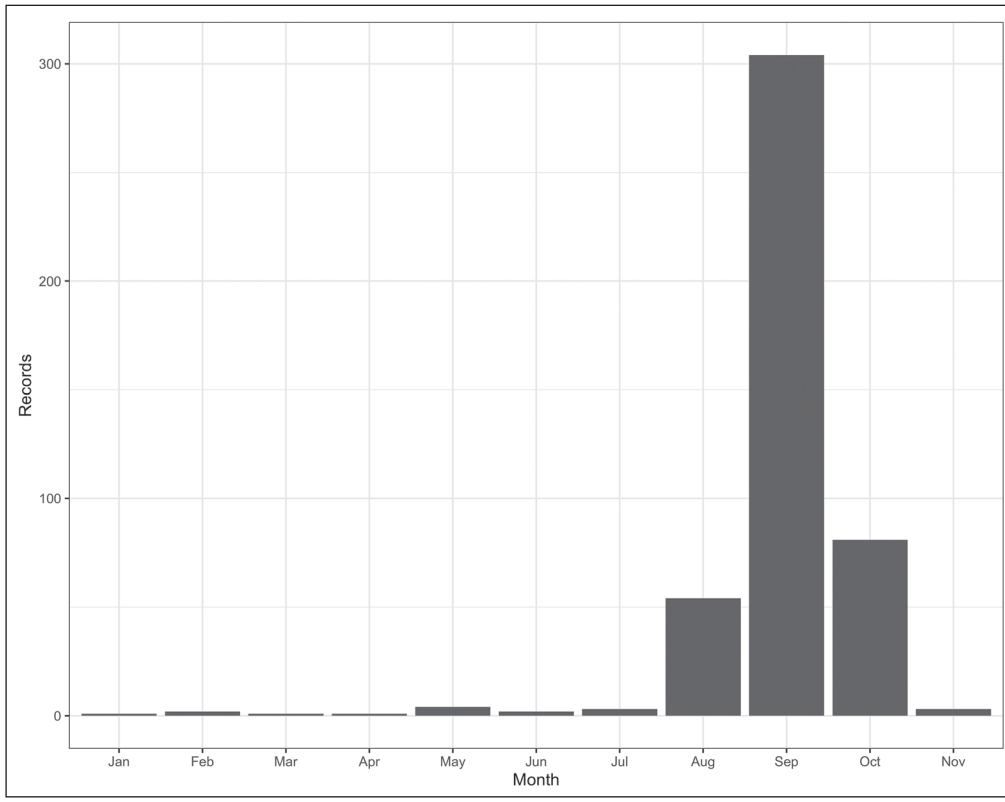

Figure 3. Temporal activity of *Andrena asteris* based on all specimen records from the Global Biodiversity Information Facility (GBIF), Symbiota Collections of Arthropods Network (SCAN), and the American Museum of Natural History's Arthropod Easy Capture Specimen database (AMNH-AEC), by month of collection.

predictive performance was obtained using jackknife partitioning (linear, quadratic, and hinge feature classes and a regulation multiplier of 3; AUC = 0.88). The AUC of the model we selected was higher than 99% of the null model iterations, and in addition to its predictive performance, was highly supported based on its small ΔAICc (1.15). The first principal component, weakly influenced by many of the bioclimatic variables, contributed most to the model predictions and the fourth principal component contributed the second most. The latter was strongly correlated with soil sand content and increased with higher sand and lower clay composition. Areas of moderate to high habitat suitability extend east from Oklahoma to the Atlantic Coast of the US and north into New Brunswick, Canada (Fig. 5). Areas of peak habitat suitability are in rough proximity to coastal and inland shorelines and major water courses with low suitability at high elevations and in the southeastern US (Fig. 5).

Nest architecture and soil texture analysis

Nests extended straight downward through a sandy surface layer that was 10–20 cm thick (Figs. 6–8). In some nests, the initial part of the tunnel was lined with a thin (~1-mm) layer of sandy loam from the deeper part of the nest. Once the nest tunnel entered the sandy loam layer at ~10–20 cm underground (Figs. 6–8), the burrow continued straight, meandering only slightly around objects, down to the depth of the cells. The vertical main tunnel varied from 5.5 to 6 mm in diameter.

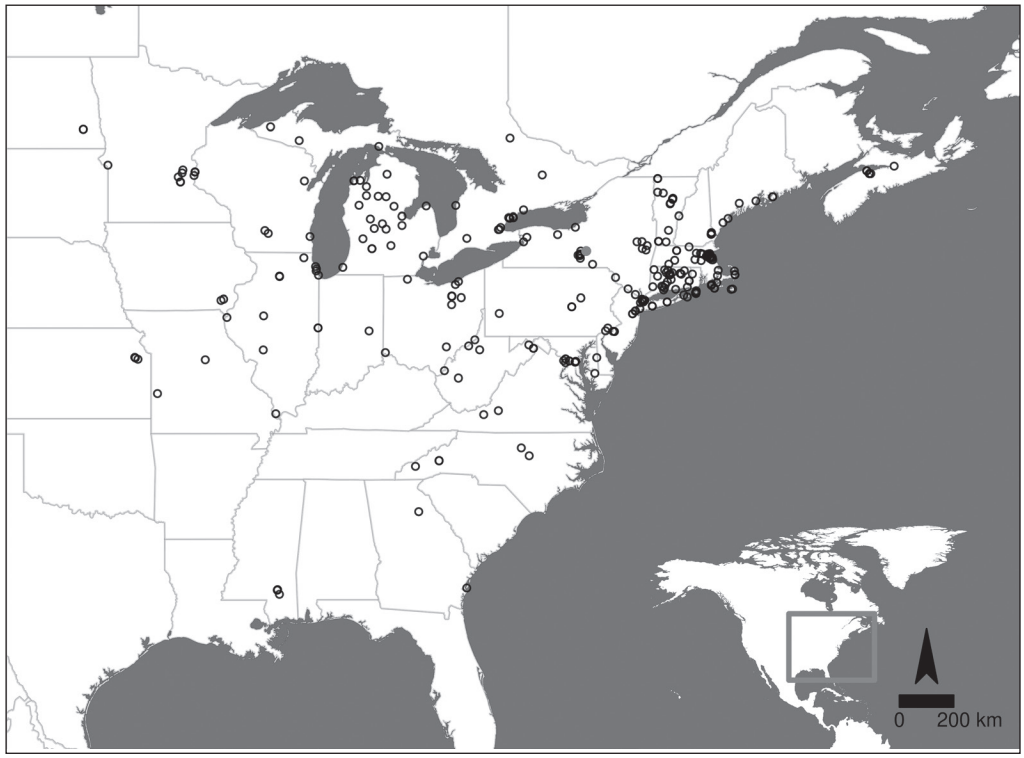

Figure 4. Spatial distribution of specimen records from all 3 data sources (SCAN+GBIF+AMNH), made with R. Same data as in Figure 3. The study site is indicated with a filled red dot.

Each nest contained from 1 to 5 brood cells in various stages of completion from partially provisioned brood cells to closed brood cells with eggs, and larvae in various stages of development. Brood cells were recovered at depths varying from 50 to 91 cm (mean = 81.06 ± 14.81, n = 18; Fig. 6). Cells were located 4–10 cm from the main burrow on a horizontal lateral tunnel and were randomly scattered around the main tunnel (Fig. 6). Brood cells were 6–8 mm in width (mean = 7.16 ± 1.02, n = 3) and 11–12 mm in length (mean = 11.73 ± 0.59, n = 3), based on 3 brood cells that were precisely measured with a digital caliper. Brood cells had a clearly visible waterproof glandular coating which was thicker toward the back of the brood cell and became progressively thinner toward the entrance of the brood cell (Fig. 8). All of the 13 intact pollen provisions recovered consisted of a relatively solid spherical mixture of pollen plus nectar, as in many Andrenidae (Danforth et al. 2019). Eggs and larvae were on top of the pollen provisions, and fully fed larvae were observed resting on their dorsum.

Pollen analysis

Consistent with expectations, all pollen found in all subsamples of all 3 pollen provisions contained exclusively pollen from flowers in the family Asteraceae. However, we were unable to reliably differentiate among genera or species of Asteraceae at the site based on univariate and multivariate analysis of the data (see Fig. S3 in Supplemental File 2). While *Solidago* spp. inflorescences were the most numerically abundant by far, the number of other Asteraceae blooming at the site

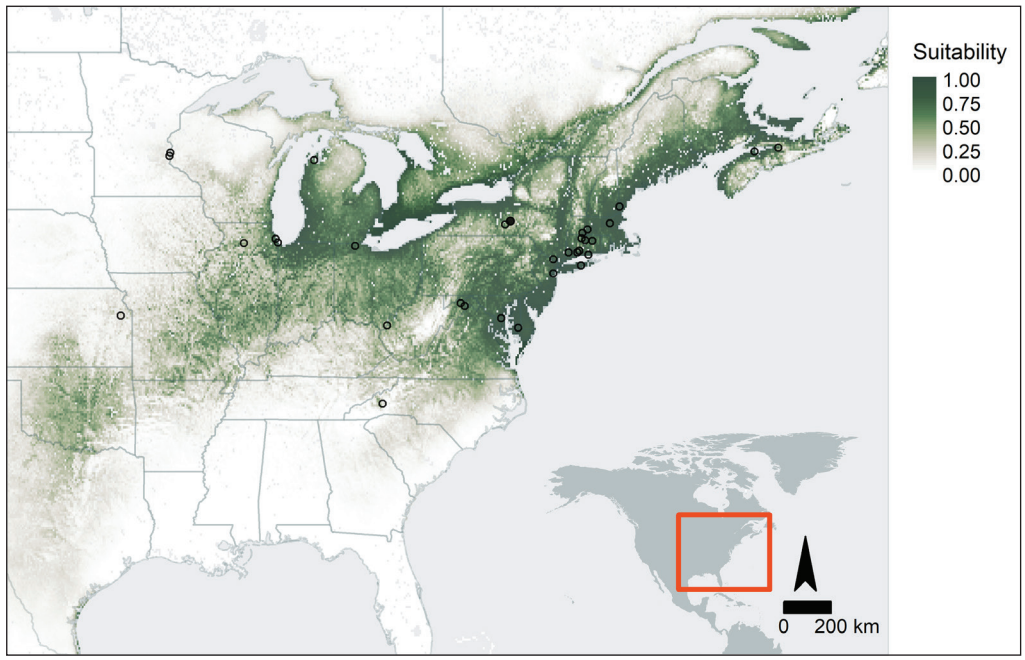

Figure 5. The modeled distribution of suitable *A. asteris* habitat trained on 31 unique localities identified between 1981 and 2010 (empty circles). The study site is indicated with a filled black dot.

was non-trivial, and we cannot rule out the possibility that *A. asteris* may also use or prefer *Symphyotrichum* spp.

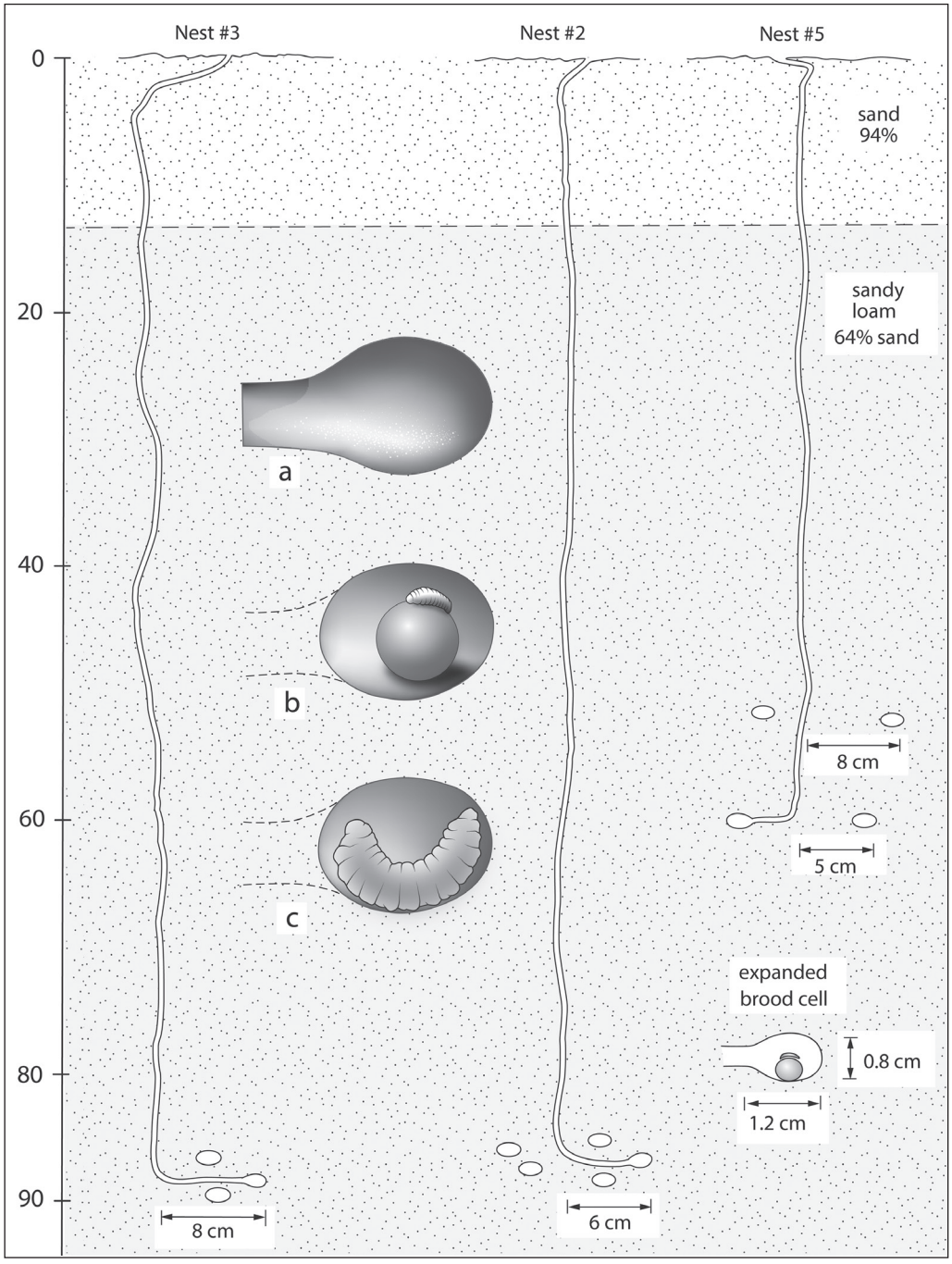

Figure 6. Diagram showing nest dimensions and brood-cell structure. (a) Empty brood cells prior to provisioning, (b) completed brood cell with pollen ball and small larva, and (c) completed brood cells with fully fed larva prior to defecation.

Parasitism

Adult *Nomada banksi* Cockerell (Fig. 1b) were common at the site and were observed inspecting nest entrances and entering nests of *A. asteris*. In one case, we discovered a living female *N. banksi* in an old, partially provisioned brood cell of *A. asteris* at a depth of ~90 cm. Our observations strongly suggest that *N. banksi* is a brood parasite of *A. asteris*. Other brood parasites seen flying in the area included *Triepeolus pectoralis* (Robertson), and various species of *Sphecodes*, *Epeolus,* and *Coelioxys*.

Discussion

Phenology and geographic distribution

Analysis of historical collection records suggests *A. asteris*, like many *Callandrena* species (Larkin et al. 2008), is a late-summer bee. Based on the Larkin et al. (2008) review of *Andrena* phenology and host-plant use, late-summer/fall foraging has arisen repeatedly (up to 4 times) in *Callandrena*, and *A. asteris* is nested within a clade of other species that emerge in late-summer to fall.

Our analysis of historical collection records also indicates that *A. asteris* has a broad geographic distribution across the eastern US, east of the 100th meridian (Fig. 4). However, our species-distribution modeling indicates that the highest habitat suitability occurs near large inland water bodies or the coast (Fig. 5). Areas of moderate to high suitability correspond to low-elevation areas with high sand and moderately low clay content in the soil.

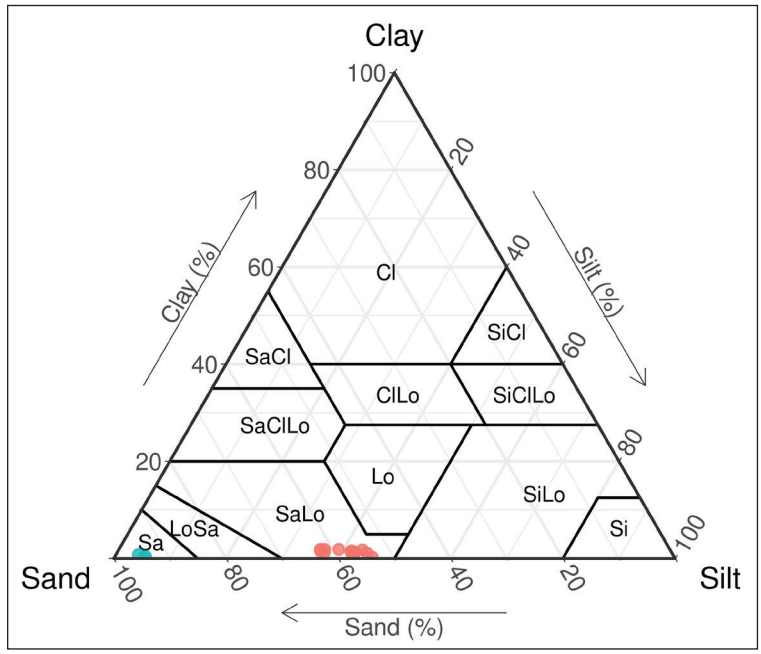

Figure 7. Texture analysis of soil taken near surface (~5 cm below surface; blue dots) and at level of brood cells (60–90 cm below surface; red dots). Soil at surface is comprised largely of pure sand whereas subsurface soils, where brood cells are located, is composed of sandy loam (Sa = Sand, Cl = clay, Si =silt, Lo = loam). The sandy loam layer starts at ~10–20 cm below the surface. Soil triangle and phenology plot were made in R using the 'ggplot2' and 'ggtern' packages (Hamilton and Ferry 2018, R Core Team, 2021, Wickham, 2016).

Nest architecture and soil-texture analysis

Andrena asteris females build nests that are up to 91 cm deep. The females themselves are between 1.2 and 1.3 cm in length, so the nest is built to a depth of as much as 72 average female body lengths. This feat is equivalent to a 1.8-m (6-ft) tall human digging a 132-m (432-ft) deep tunnel. To the best of our knowledge this

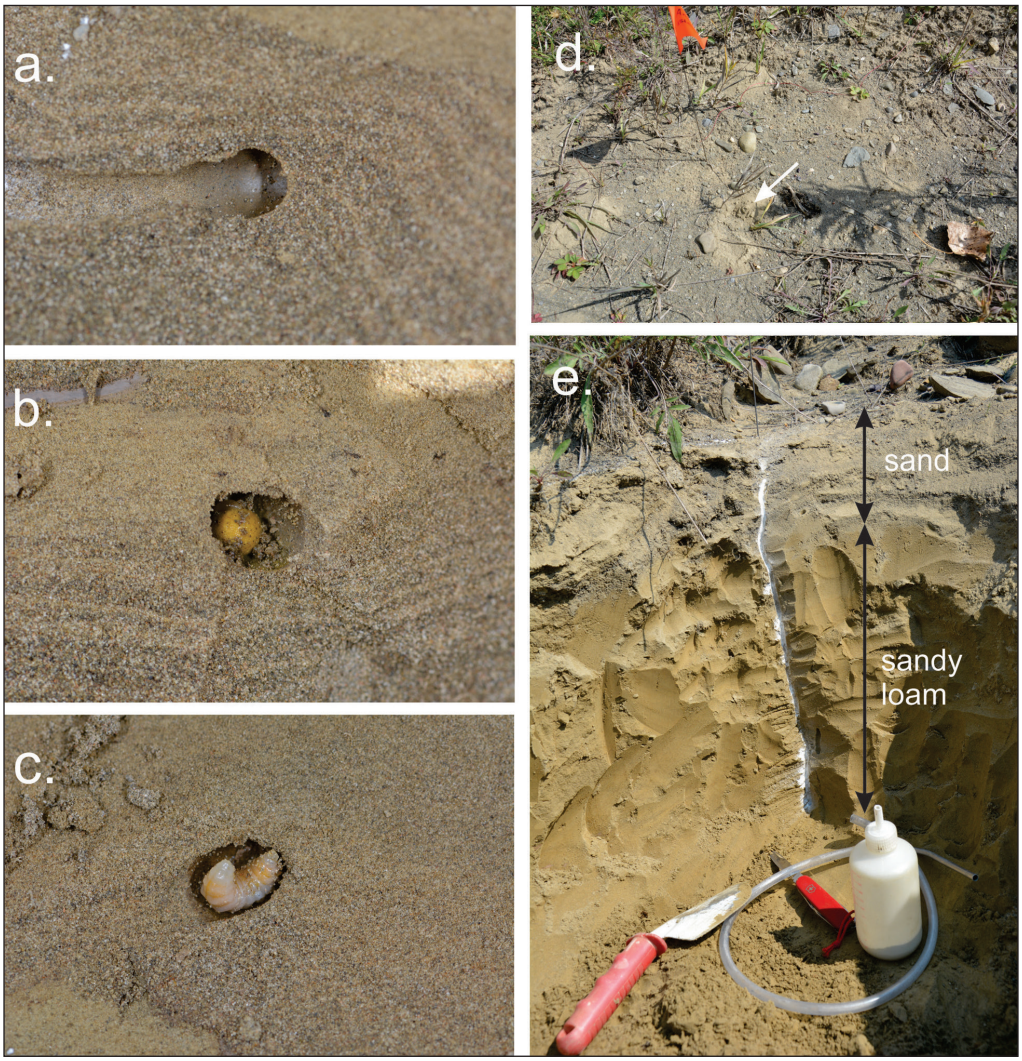

Figure 8. Photos of nest architecture: (a) brood cell showing cell lining, (b) pollen ball with small larva, (c) fully developed larva, (d) nest entrance (indicated by arrow), and (e) main burrow extending downward through upper sand layer and into lower sandy loam layer.

Figure 9 (following page). Brood-cell depth in *Andrena* species. Data from Cane and Neff (2011). Species ranked by the midpoint of the range of brood-cell depths. Species of *Callandrena* Group A (= *Callandrena* sensu stricto) in black; species of *Callandrena* Groups B–D (= Pisanty et al. Group 12) in orange; other *Andrena* in grey. *Andrena asteris* is highlighted in red.

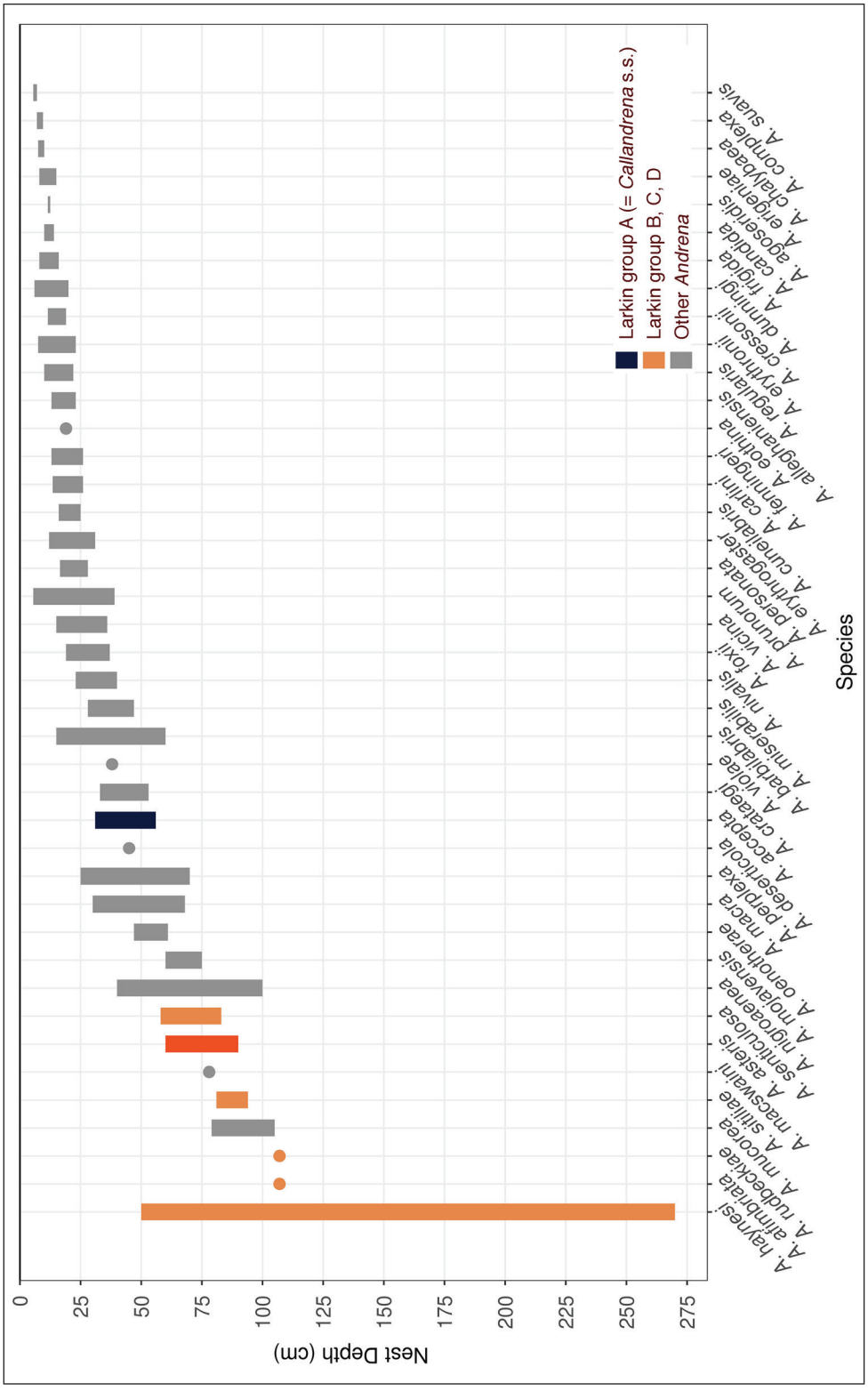

Figure 9. [Caption on preceding page.]

is the deepest solitary bee nest recorded in northeastern North America, although some communally nesting or more highly social ground-nesting species in the region have built deeper ones (Cane and Neff 2011:supplementary material).

In order to compare depth of brood cells in *A. asteris* to other members of the genus, we utilized data assembled by Cane and Neff (2011) on the brood-cell depths of various ground-nesting bee species. For *Andrena*, there are a total of 41 observations of brood-cell depth (Fig. 9). Brood-cell depths vary widely in *Andrena*, from a minimum of 5.5 cm (in *Andrena* [*Ptilandrena*] *suavis* Timberlake; Linsley and MacSwain 1959) to a maximum of 270 cm (in *Andrena* [*Callandrena*] *haynesi* Viereck and Cockerell; Parker and Griswold 1982). *Andrena asteris* ranks seventh in median brood-cell depth out of the 41 species included in the Cane and Neff (2011) dataset (Fig. 9). Interestingly, there is a clear phylogenetic component as well. All members of *Callandrena* Group B,C,D exhibit very deep brood cells. Six of the top 10 deepest nests include species of *Callandrena* Group B,C,D, including *Andrena asteris* (Fig. 9). The only species in the dataset in *Callandrena* sensu stricto (Group A of Larkin et al. 2006), *Andrena* (*Callandrena*) *accepta* Viereck (Rozen 1973), a communal bee, builds a much shallower nest (Fig. 9). Deep nests are hypothesized to be an adaptation to nesting in sandy, dune-like habitats (Parker and Griswold 1982), such as the glacial moraine at our site, where the surface layer of the soil is likely to shift over time.

Our soil-texture analysis revealed that the nests of *A. asteris* were built through a surface layer of essentially pure sand followed by sandy loam with almost no clay content (Figs. 6–8). Sandy loam soils retain heat because of the low water content of these soils (R. Schindelbeck, Cornell Soil Health Laboratory, Ithaca, NY, pers. comm.), which may facilitate bee larval development either early or late in the year. For a late-summer bee nesting in the northeastern US, the deep brood cells and sandy loam soil texture could provide additional protection against winter freezing.

The soil texture we observed *A. asteris* nesting in is comparable to the preferences of other species of Andrenidae reported in Cane (1991). Many andrenid bees construct nests in sandy loam, and *Andrena* (*Plastandrena*) *prunorum* Cockerell prefers essentially pure sand (Cane 1991). Without additional observations of nesting sites of *A. asteris*, it is impossible to say if females of this species are preferentially selecting soils with the texture we observed at our site, but the unique texture of the soil and the depth at which nests are constructed would suggest that they have particular soil requirements that might put limits on their spatial distribution and abundance.

Pollen analysis

Our pollen identification supports the hypothesis that *A. asteris* is an Asteraceae specialist, consistent with historical collection records (LaBerge 1967). Despite challenges separating these taxa morphologically, we are confident that the most-likely host plants are goldenrods or asters in the genera *Solidago*, *Symphyotrichum*, and/or *Euthamia*. Asteraceae are important late summer floral resources in the eastern US. While spring emergence is the ancestral trait in North American *Andrena*,

11 of the 14 species of *Callandrena* that occur east of the Mississippi are late summer/fall-active (Larkin et al. 2008) during the period when the majority of floral resources available are Asteraceae. Asteraceae pollen has been shown to be relatively unpalatable to honey bees, bumble bees, and some *Colletes* species (Loper and Cohen 1987, Müller and Kuhlmann 2008, Vanderplanck et al. 2020); it lacks amino acids essential to honey bee brood development and may be both mechanically and chemically protected (Loper and Cohen 1987, Vanderplanck et al. 2020; but see Giacomini et al 2018 for medicinal benefits of sunflowers to bumble bees). *Andrena* do not seem to be so discriminating. Asteraceae specialization has evolved at least 4 times in the genus (Larkin et al. 2008), and some generalist *Andrena* use Asteraceae pollen despite its difficulties for other taxa (Wood and Roberts 2018).

Parasitism

Ascher et al. (2014) hypothesized, based on phenology, that *Nomada banksi* could be a brood parasite of *A. asteris*. Our results corroborate this hypothesis based on observations of *N. banksi* within the nests of *A. asteris*.

Conservation status

In a recently released statewide assessment of the conservation status of focal New York pollinators, White et al. (2022) ranked *Andrena asteris* as S3, meaning "vulnerable" (defined as "at moderate risk of extirpation in the jurisdiction due to a fairly restricted range, relatively few populations or occurrences, recent and widespread declines, threats, or other factors"). While our study of a single population cannot directly assess the conservation status of *A. asteris*, our analysis of voltinism, nesting biology (including soil texture), and host-plant use would suggest that this bee exhibits life-history traits that would render it of conservation concern. Previous studies indicate that univoltine bees that are host-plant specialists are more vulnerable than either multivoltine or generalist species. In a study of historical trends in bee abundance and species richness in Britain and the Netherlands, Biesmeijer et al. (2006) found that habitat and floral specialists and univoltine bees were the most likely to be in decline. Likewise, Burkle et al. (2013), in a comparison of contemporary and historical bee communities in the midwestern US, found that specialists were more likely to experience extinction than generalists, despite the fact that the host-plants of the specialists were still present. Finally, Bogush et al. (2020), in a study of bees from the Czech Republic, found that oligolectic bees (host-plant specialists) were proportionally more commonly represented in the IUCN Red List of threatened bees than generalists. Furthermore, several studies (summarized in Danforth et al. 2019:66) indicate that *Andrena* often have very low per-capita offspring production. Female *Andrena* have relatively short adult lifespans and provision fewer than 1 offspring per day (Franzén and Larsson 2007, Giovanneti and Lasso 2005). These 2 factors together presumably result in low (<10) lifetime fecundity for many species of *Andrena*. In summary, species of *Andrena* with narrow host-plant preferences and unique soil and habitat requirements like *A. asteris* are likely of conservation concern.

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Literature Cited

Aiello-Lammens, M.E., R.A. Boria, A. Radosavljevic, B. Vilela, and R.P. Anderson. 2015. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38(5):541–545.

Ascher, J.S., and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila); draft 55; updated on 17 November 2020. Available online at http://www.discoverlife.org/mp/20q?guide=Apoidea_species.

Ascher, J.S., S. Kornbluth, and R.G. Goelet. 2014. Bees (Hymenoptera: Apoidea: Anthophila) of Gardiners Island, Suffolk County, New York. Northeastern Naturalist 21(1):47–71.

Biesmeijer, J.C., S.P.M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, J. Settele, and W.E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313(5785):351–354.

Bogusch, P., E. Bláhová, and J. Horák. 2020. Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. Arthropod-Plant Interactions 14(6): 759–769.

Bossert, S., T.J. Wood, S. Patiny, D. Michez, E.A.B. Almeida, R.L. Minckley, L.Packer, J.L. Neff, et al. 2021. Phylogeny, biogeography, and diversification of the mining bee family Andrenidae. Systematic Entomology 2021:1–20.

Burkle, L.A., J.C. Marlin, and T.M. Knight. 2013. Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. Science 339(6127):1611–1615.

Cane, J.H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): Texture, moisture, cell depth, and climate. Journal of the Kansas Entomological Society 64(4):406–413.

Cane, J.H. 2018. Co-dependency between a specialist *Andrena* bee and its death camas host, *Toxicoscordion paniculatum*. Arthropod–Plant Interactions 12:657–662.

Cane, J.H., and J.L. Neff. 2011. Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. Biological Conservation 144(11):2631–2636.

Danforth, B.N., R.L. Minckley, and J.L. Neff. 2019. The Solitary Bees: Biology, Evolution, Conservation. Princeton University Press, Princeton, NJ. xi + 472 pp.

de Marco, P., and C.C. Nóbrega. 2018. Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. PLoS ONE 13(9):e0202403.

Dubitzky, A., J. Plant, and K. Schönitzer. 2010. Phylogeny of the bee genus *Andrena* Fabricius based on morphology. Mitteilungen der Münchner Entomologischen Gesellschaft 100:137–202.

Faegri, K., P.E. Kaland, and K. Krzywinski. 1989. Textbook of Pollen Analysis, 4th Edition. Wiley, Chischester, UK. 328 pp.

Feng, X., D.S. Park, Y. Liang, R. Pandey, and M. Papeş. 2019. Collinearity in ecological niche modeling: Confusions and challenges. Ecology and Evolution 9(18):10365–10376.

Franzén, M., and M. Larsson. 2007. Pollen harvesting and reproductive rates in specialized solitary bees. Annales Zoologici Fennici 44(6):405–414.

Giacomini, J.J., J. Leslie, D.R. Tarpy, E.C. Palmer-Young, R.E. Irwin, and L.S. Adler. 2018. Medicinal value of sunflower pollen against bee pathogens. Scientific Reports 8(1):1–10.

Giovanetti, M., and E. Lasso. 2005. Body size, loading capacity, and rate of reproduction in the communal bee *Andrena agilissima* (Hymenoptera; Andrenidae). Apidologie 36(3):439–447.

Hamilton, N.E., M. Ferry. 2018. ggtern: Ternary diagrams using ggplot2. Journal of Statistical Software, Code Snippets 87(3):1–17.

Hengl, T. 2018a. Sand content in % (kg / kg) at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution. [Data set]. Available online at https://doi.org/10.5281/zenodo.2525662. Accessed 26 May 2022.

Hengl T. 2018b. Clay content in % (kg / kg) at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution. [Data set]. Available online at https://doi.org/10.5281/zenodo.2525663. Accessed 26 May 2022.

Karger, D.N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R.W. Soria-Auza, N.E. Zimmermann, H.P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the earth's land-surface areas. Scientific Data 4:1–20.

Kass, J.M., R. Muscarella, P.J. Galante, C.L. Bohl, G.E. Pinilla-Buitrago, R.A. Boria, M. Soley-Guardia, and R.P. Anderson. 2021. ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution 12(9):1602–1608.

LaBerge, W.E. 1967. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part I. *Callandrena* (Hymenoptera: Andrenidae). Bulletin of the University of Nebraska State Museum 7:1–318.

Larkin, L.L. 2004. Four new fall species of *Andrena* from the southwestern United States (Hymenoptera: Andrenidae). Journal of the Kansas Entomological Society. 77(3):254–268.

Larkin, L.L., J.L. Neff, and B.B. Simpson. 2006. Phylogeny of the *Callandrena* subgenus of *Andrena* (Hymenoptera: Andrenidae) based on mitochondrial and nuclear DNA data: Polyphyly and convergent evolution. Molecular Phylogenetics and Evolution 38(2):330–343.

Larkin, L.L., J.L. Neff, and B.B. Simpson. 2008. The evolution of a pollen diet: Host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). Apidologie 39(1):133–145.

Linsley, E.G., and J.W. MacSwain. 1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. University of California Publications in Entomology 16:1–46.

Loper, G.M., and A.C. Cohen. 1987. Amino acid content of dandelion pollen, a honey bee (Hymenoptera: Apidae) nutritional evaluation. Journal of Economic Entomology 80(1):14–17.

Müller, A., and M. Kuhlmann. 2008. Pollen hosts of western Palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): The Asteraceae paradox. Biological Journal of the Linnean Society 95(4):719–733.

Natural Resource Conservation Service (NRCS). 2019. Web soil survey. Available online at https://websoilsurvey.sc.egov.usda.gov. Accessed 21 October 2020.

Neff, J.L., and B.B. Simpson. 1997. Nesting and foraging behavior of *Andrena (Callandrena) rudbeckiae* Robertson (Hymenoptera: Apoidea: Andrenidae) in Texas. Journal of the Kansas Entomological Society 70(2):100–113.

Parker, F.D., and G.E. Bohart. 1982. Notes on the biology of *Andrena (Callandrena) helianthi* Robertson (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 58:111–116.

Parker, F.D., and T.L. Griswold. 1982. Biological notes on *Andrena (Callandrena) haynesi* Viereck and Cockerell (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 58(4):284–87.

Phillips, S.J., M. Dudík, and R.E. Schapire. 2022. Maxent software for modeling species niches and distributions. Version 3.4.3. Available online at https://biodiversityinformatics.amnh.org/open_source/maxent/.

Pisanty, G., R. Richter, T. Martin, J. Dettman, and S. Cardinal. 2021. Molecular phylogeny, historical biogeography, and revised classification of andrenine bees (Hymenoptera: Andrenidae). Molecular Phylogenetics and Evolution 170:107151.

Punt, W., and P.P. Hoen. 2009. The northwest European pollen flora, 70: Asteraceae – Asteroideae. Review of Palaeobotany and Palynology 157(1–2):22–183.

QGIS.org. 2022. QGIS Geographic Information System. QGIS Association. Version 3.16. Available online at http://www.qgis.org.

R Core Team, 2021. R: A language and environment for statistical computing. Version 4.1.2. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/.

Radosavljevic, A., and R.P. Anderson. 2014. Making better Maxent models of species distributions: Complexity, overfitting, and evaluation. Journal of Biogeography 41(4):629–643.

Rozen, J.G. 1973. Biology notes on the bee *Andrena accepta* Viereck (Hymenoptera, Andrenidae). Journal of the New York Entomological Society 81(1):54–61.

Rozen, J.G., Jr., B.N. Danforth, C.S. Smith, B.L. Decker, N.N. Dorian, D. Dority, S.K. Kilpatrick, E. Krichilsky, A.N. Laws, and K. Urban-Mead 2019. Early nesting biology of the bee *Caupolicana yarrowi* (Cresson) (Colletidae: Diphaglossinae) and its cleptoparasite *Triepeolus grandis* (Friese) (Apidae: Nomadinae). American Museum Novitates 3931:1–20.

Sillero, N., and A.M. Barbosa. 2021. Common mistakes in ecological niche models. International Journal of Geographical Information Science 35(2):213–226.

Swink, W.G., S.M. Paiero, and C.A. Nalepa. 2013. Buprestidae collected as prey by the solitary, ground-nesting philanthine wasp *Cerceris fumipennis* (Hymenoptera: Crabronidae) in North Carolina. Annals of the Entomological Society of America 106(1):111–116.

Vanderplanck, M., H. Gilles, D. Nonclercq, P. Duez, and P. Gerbaux. 2020. Asteraceae paradox: Chemical and mechanical protection of *Taraxacum* pollen. Insects 11(5):304.

White, E.L., M.D. Schlesinger, and T.G. Howard. 2022. The Empire State native pollinator survey (2017–2021). New York Natural Heritage Program, Albany, NY. Available online at https://www.nynhp.org/projects/pollinators/. Accessed 20 July 2022.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, NY. Available online at https://ggplot2-book.org/.

Wood, T.J., and S.P. Roberts. 2017. An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. Biological Conservation 215:72–80.

Wood, T.J., and S.P. Roberts. 2018. Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. Biological Journal of the Linnean Society 124(4):732–746.

Zizka, A., D. Silvestro, T. Andermann, J. Azevedo, C. Duarte Ritter, D. Edler, H. Farooq, A. Herdean, M. Ariza, R. Scharn, et al. 2019. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution 10(5):744–751.